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Nesting Biology of a Tropical Myrmicine Ant, *Myrmicaria arachnoides* (Formicidae), in West Java, Indonesia

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Abstract.—Nesting biology of a myrmicine ant, *Myrmicaria arachnoides*, was studied on Java island, Indonesia. The colonies were polydomous and polygynous. Nests of a colony were located close to each other on different leaves of a tree. The number of dealated queens was positively correlated with the numbers of nests, adult workers and immatures, but not with the numbers of males and new queens present. Adaptive aspects of nesting site, polygyny and polydomy are discussed.

The genus *Myrmicaria* is widely distributed in the Old World tropics, i.e., Southeast Asia, South Asia and tropical Africa. Emery (1922) sorted *Myrmicaria* species into two principal groups based on morphology, i.e., the *M. brunnea* group and *M. arachnoides* group, and briefly mentioned that species of the former construct huge nests underground while those of the latter construct carton nests on trees. Our observations have confirmed this for most of the Southeast Asian forms (also see Karavaiev 1935). However, there are few detailed studies on the nesting habits of *Myrmicaria*. In Cameroon, Africa, one species, *M. opaciventris* Emery, belonging to the *M. brunnea* group, has been intensively studied for its ecology/bionomics including nesting habits (Kenne and Dejean 1999, Kenne et al. 2000, 2001). This species has polydomous and polygynous colonies in the soil. Interconnected nests are built and trenches and tunnels are constructed as underground trails connecting nests. Species of the *M. arachnoides* group also often construct polydomous and polygynous colonies but on vegetation (Karawajew 1935, this study, Bakhtiar and Yamane unpubl.). This may allow them to develop relatively large colonies similar to *Polyrhachis* species nesting in similar situations (R. Kohout pers. com.).

Research on colony growth in eusocial insects has focused on the relationship between colony size and productivity. At each growth period, colonies make investment decisions about whether to produce more workers and grow larger, or rather to invest that energy in reproductive output (Billick 2001). Because colony size is often the most important factor determining reproductive output (Odum and Pontin 1961, Michener 1964, Fowler 1986, Tschinkel 1993, Savolainen et al. 1996), maximizing the long-term size of the colony is an important component of colony fitness (Oster and Wilson 1978). Colony size is known to be related with queen number and also to affect caste/sex composition in ant nests. In this respect nesting behaviour of the *M. arachnoides* group is of special interest.

Little has been studied on the colony structure of the Southeast Asian *Myrmicaria arachnoides* F. Smith (but see Karavaiev 1935). During our study on the taxonomy of Oriental *Myrmicaria* we obtained relatively good samples of *M. arachnoides* colonies on Java island, Indonesia. We report here the nesting sites, colony size, and reproductive output of these colonies.

MATERIALS AND METHODS

The taxonomy of *Myrmicaria* is still unresolved, particularly the status of infraspecific forms of some species. *Myrmicaria arachnoides* was originally described from Borneo and consists of several 'subspecies' (Bolton 1995), of which at least some would be good species. The form studied here is in coloration most similar to '*M. arachnoides arachnoides*'.

Samples were collected from three disturbed sites in West Java in September 2004: foot of G. Salak – Site 1 (6°39′ S, 106°46′ E, 560 m) (BOG3, 10 & 18), Salak-Halimun Corridor – Site 2 (6°45′S, 106°37′E, 710 m) (BOG24, 25 & 26), and Bogor Botanical Garden – Site 3 (6°36′S, 106°48′E, 220 m) (BOG 38). The distance between each plant where these colonies were found was approx. 5–50 m in Site 1, and 5–10 m in Site 2. These habitats have been infringed by plantation or agricultural activities or surrounded by residential areas. Nests constructed on a same plant were thought to constitute a single colony as the ants use same foraging trails. Nests of each colony from different plants were collected intact and put into plastic bags separately. In total, seven colonies of different sizes were collected.

Nests were measured for their maximum width and length, and then dissected carefully. Workers, reproductives (dealated queens, young winged queens and males), immatures (eggs, larvae and pupae) were counted and preserved in 80% alcohol. Pupae were sorted into sexes and castes as much as possible.

RESULTS

Nesting site and structure.—In Salak and Salak-Halimun Corridor, colonies were found in plantation areas with sparse trees and bushes, while in the botanical garden they were found in a forested area with relatively high trees. Nests were located on the underside of leaves of various plant species at 0.5–1.5 m above the ground in the former two sites (Fig 1 a,b), but in the botanical garden they were positioned higher at around 3–4 m above the ground. In the case of polydomous colonies component nests were generally constructed separately on different leaves of the same plant, but in one case, two nests were built narrowly connected on one and the same leaf (BOG25-2 & -4) (Appendix 1).

Nests were made of carton-like material (probably chewed plant tissues), flattened domes in shape, and greyish brown in colour. Various sizes of nests were built on the underside of various sizes of leaves (Appendix 1). Within the nest, there were numerous chambers for adults and immatures; some of these would be used as galleries for the movements of workers (Fig. 1 b,c).

The number of nests per colony varied from 1 to as many as 12; nests of a colony were usually built close to each other on one plant (approx. 15–30 cm apart).

Colony composition.—Dealated queens (Q) were considered to be foundresses or those that have joined later (simply called 'queens' hereafter) and were found in all colonies and all nests except in BOG18-3 and BOG25-11. The two queenless nests had immatures, suggesting the transportation of them from other nests where a laying queen(s) existed. The number of queens differed from colony to colony and nest to nest (Fig. 2). Number of queens is highly correlated with the number of nests (Fig. 3a). The highest mean number of queens per nest, 11.67, was found in a 3-nest colony (BOG18) (range: 0–22) (Fig. 2). However, BOG38 which also had 3 nests had the smallest number of queens in each of the

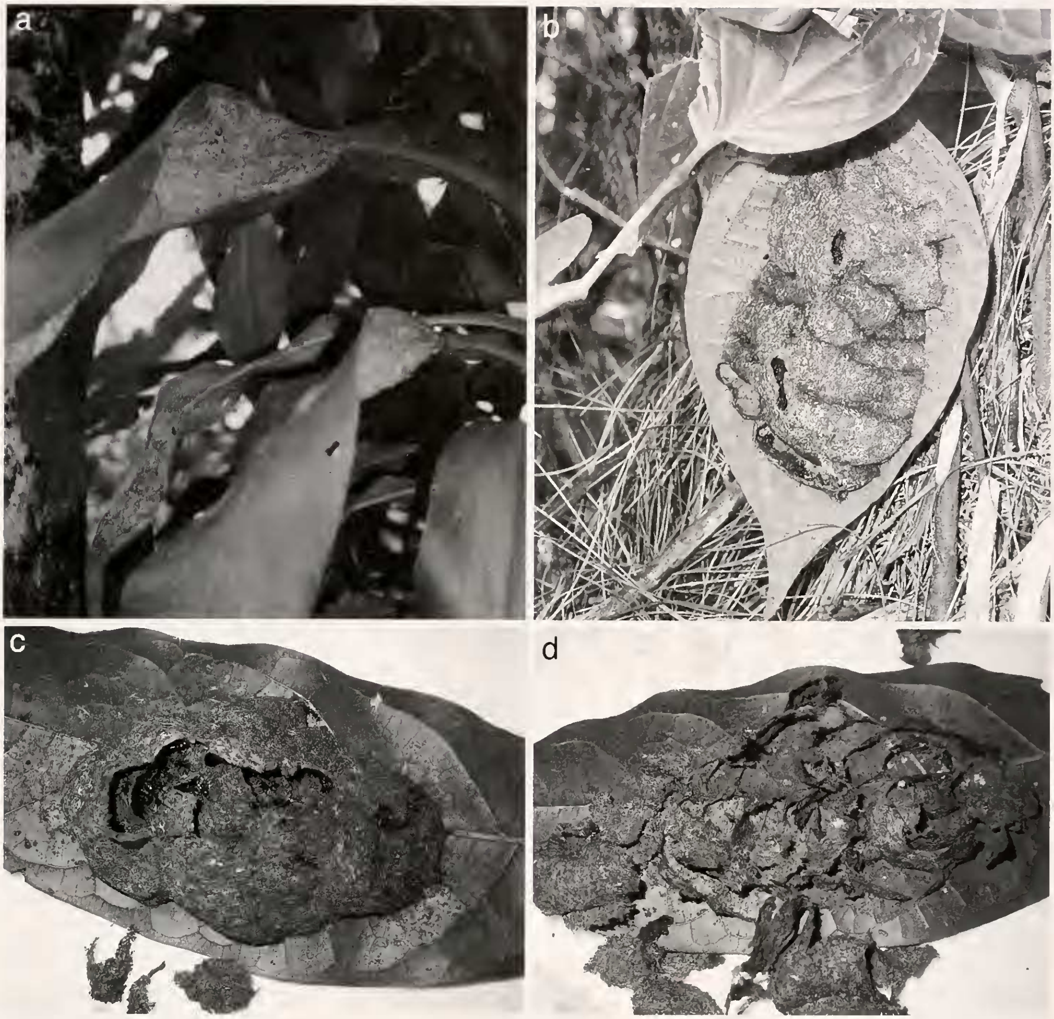

Fig. 1a–d. a, Nests constructed on underside of leaves. b, Nest on the underside a leaf. c, Structure of a nest; top of envelop removed to show the interior. d, Compartments within nest; outer walls removed.

nests (mean=1.33 with a range of 1 to 2). BOG24 (1-nest colony) and BOG3 (2-nest colony) contained relatively small numbers (1–3) of queens per nest. In larger colonies, BOG10 (4-nest colony) and BOG25 (12-nest colony), the mean number of queens per nest was larger and relatively stable (4.00 ± 2.16 & 4.00 ± 3.34 respectively).

Within each colony, workers represent the greatest number among inhabitants (approx. 40%) except in BOG 25 and BOG26 (approx. 30.3%), followed by eggs (approx. 20–40%) and larvae (approx. 10–30%). Worker pupae and male adults constitute relatively lower ratios, while other life forms (stages) were much fewer.

Most of the nests had queen(s), workers and immatures, and there was no striking specialization for a certain nest(s) in a single colony with respect to worker/reproductive production. However, BOG18-3, BOG38-1, BOG26-3 and BOG10-2 contained higher percentages of workers compared with other nests composing these colonies (Appendix 1).

In the single 1-nest colony (BOG24), all the adults were workers (approx. 40% of all the inhabitants) except for three queens

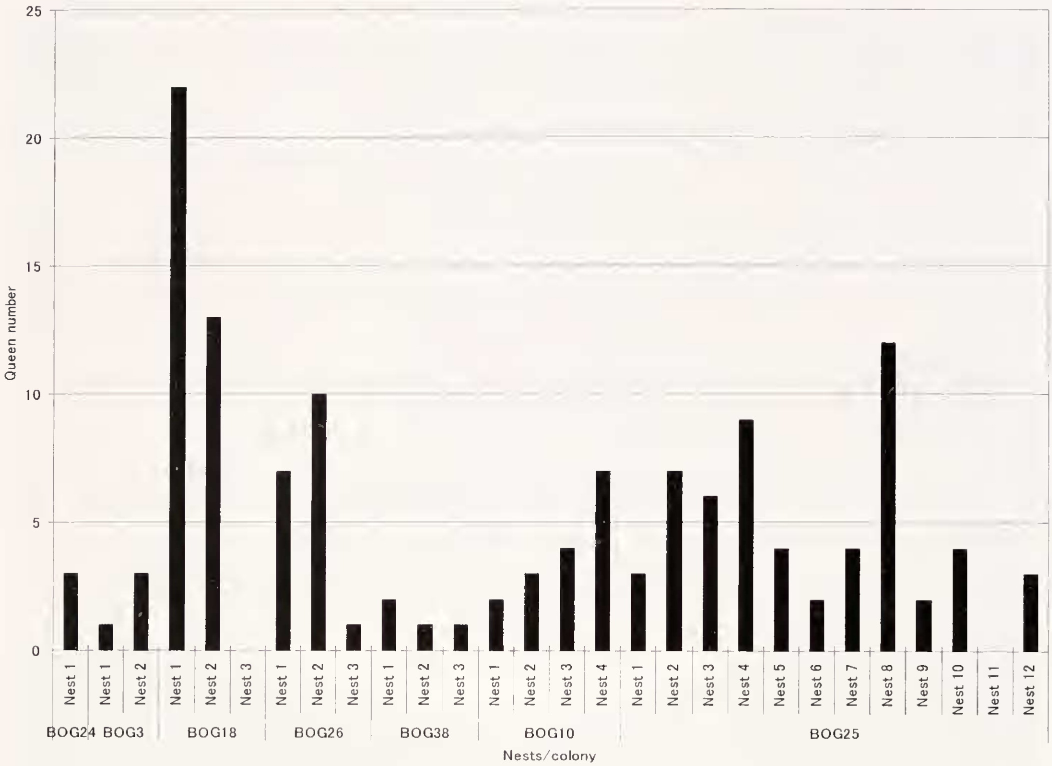

Fig. 2. Number of queens in each nest and colony.

that were possibly egg layers. There were numerous eggs (approx. 45%), while larvae and pupae were relatively few, being approx. 10% and 5%, respectively. Furthermore, all the pupae were workers, all this suggesting that the colony was in its ergonomic stage (reproduction and dispersal are not its immediate concern) (cf. Oster and Wilson 1978).

In the single 2-nest colony (BOG3) all life stages were present except the pupae of new queens (Appendix 1). Males had started to be produced, representing approximately 5% of the total adults for the colony (Appendix 1). Male pupae also existed in BOG3-1 (Appendix 1). Adult workers, eggs and larvae each had similar percentages for the whole colony and also for each component nest.

In the three 3-nest and 4-nest colonies (BOG18, 26 and 38), all life stages were present except the pupae of new queens (in all colonies), and winged adult queens in colony BOG26 (Appendix 1). As in smaller colonies mentioned earlier, workers again constitute between 30 and 40% of all inhabitants. Following the workers, eggs and larvae also occupied large proportions except in BOG18-3, just as in the smaller colonies. In BOG18-3, more adult males were observed. Worker pupae were observed to constitute approximately 5% in the colonies BOG38 and BOG26.

In the 12-nest colony (BOG25; Appendix 1), winged queens were seen only in two nests in small numbers, while males were distributed more evenly; the pupae of new queens were absent in this colony. For the whole colony, workers, eggs and larvae had approximately the same numbers (around 30%) while approximately 10% were worker pupae.

Reproductive output.—There were strong relationships between the number of

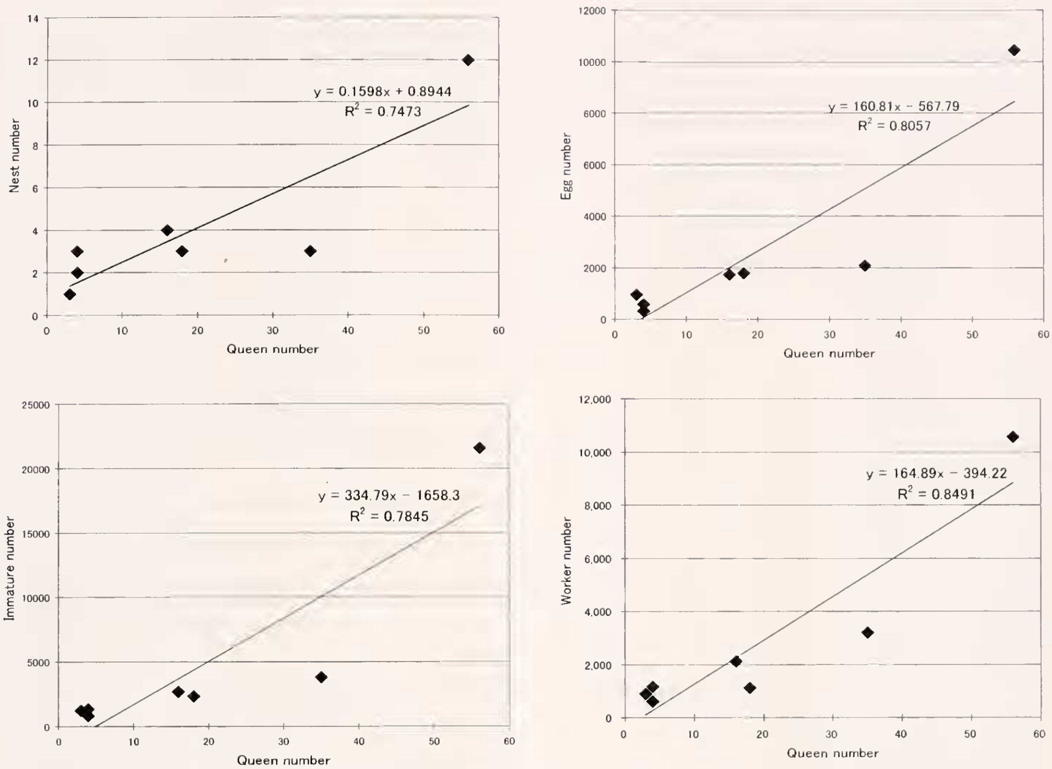

Fig. 3a–d. a, Correlation between queen and nest numbers. b, Correlation between queen and egg numbers. c, Correlation between queen and immature numbers. d, Correlation between queen and worker numbers.

queens and those of workers and immatures (Figs 3 b–d) (but the correlation was often strengthened by the values for the largest colony BOG25). These relationships sometimes hold also among the nests of single colonies but usually with a smaller R^2 as seen in BOG10 and BOG25 (R^2=0.0577 and 0.5549 respectively). In BOG38, however, the relationships were negative. Egg:worker ratio was relatively constant with a mean of 0.86 ± 0.5 and 0.88 ± 0.39 for each nest and colony respectively (Table 1). Number of queens was not significantly correlated with the numbers of new queens and males found in every colony (R^2=0.0919 and 0.0254 respectively).

DISCUSSION

Nesting site, nest structure and adaptation to arboreal nesting.—We found nests of *Myrmicaria arachnoides* in small remnant patches of secondary forests surrounded by human settlements and plantations, and colony/nest density was relatively high. However, not all such patches harboured this ant. Generally, nests are built of carton on the under-surface of leaves with 1–2 entrances in the outer envelope. This nesting habit may protect the nests from rain and visual predators; see Hölldobler and Wilson (1990) for other adaptive features of arboreal nests. Several colonies were found to be located close to each other but on different trees (approx. 5–10 m). Closer observations, both behavioral and genetic, are needed to clarify if they are completely independent from each other or form a kind of supercolony.

Polygyny and polydomy.—*Myrmicaria arachnoides* colonies observed in the present study clearly showed a polydomous and polygynous condition. At present it is not

Table 1. Egg:worker (E:W) ratio.

Colony	Nest	E:W ratio for nest	E:W ratio for colony	Colony	Nest	E:W ratio for nest	E:W ratio for colony
BOG24	BOG24	1.08	1.08	BOG25	BOG25(1)	1.00	0.99
BOG3	BOG3(1)	0.47	0.50		BOG25(2)	1.15	
	BOG3(2)	0.53			BOG25(3)	0.88	
BOG18	BOG18(1)	0.65	0.65		BOG25(4)	1.28	
	BOG18(2)	0.66			BOG25(5)	0.86	
	BOG18(3)	0.00			BOG25(6)	0.85	
BOG26	BOG26(1)	1.98	1.59		BOG25(7)	1.02	
	BOG26(2)	2.00			BOG25(8)	1.38	
	BOG26(3)	0.37			BOG25(9)	0.22	
BOG38	BOG38(1)	0.22	0.50		BOG25(10)	0.73	
	BOG38(2)	1.37			BOG25(11)	0.71	
	BOG38(3)	0.69			BOG25(12)	0.82	
BOG10	BOG10(1)	1.73	0.82				
	BOG10(2)	0.23					
	BOG10(3)	0.61					
	BOG10(4)	0.69					
	MEAN	0.86 ± 0.5	0.88 ± 0.39				

known whether polygyny in the present case was the result of pleometrosis (colony foundation by multiple queens) or later joining of inseminated daughters or alien females, and whether all the queens are egg layers or not. But the distribution of queens and immatures in colonies strongly suggests the existence of multiple egg layers.

Ecological factors have been invoked to explain the emergence of polygyny, in particular, high dispersal risks, high probabilities of colonies losing their queens, short queen lifespan compared to colony survivorship and low success of individual queens conducting independent colony founding (Keller 1995, Elias et al. 2005). Sudd and Franks (1987) also reasoned that queens may come together at the colony-founding stage to pool their resources during the first and most vulnerable stages in colony growth (for the advantage of pleometrosis, see also Hölldobler and Wilson, 1990).

The presence of multiple queens in nests and colonies in most of the samples studied here can be discussed in relation to nesting site and competition with other species. As mentioned above, nesting of this species (and probably of its related forms) is found in rather restricted patches of suitable habitat, but usually in high densities in the patches where they have established themselves. Successful establishment of immigrant queens may be not common, but accomplished by rapid development of colonies helped by pleometrosis and polygyny, and surviving populations will be maintained by polydomy and adoption of additional queens (for *Camponotus*, see Hansen and Klotz 2005). Thus, trees of a certain area can be dominated by this species as observed in Salak-Halimun Corridor. Although the ant fauna associated with *M. arachnoides* is not yet known, the above reasoning does not contradict the "ant mosaic" mentioned by Majer (1993), Djieto-Lordon and Dejean (1999), and others.

In polygynous colonies of *Myrmicaria arachnoides*, there is a possibility of colony reproduction due to budding (cf. Elias et al. 2005). In this case there should be a polyethism among new queens: some disperse to other patches after mating flights, and others prefer to move to nearby branches or trees with a group of workers. However, we do not have any evidence supporting this view.

Colony size and reproductive production.— Smaller colonies (eg. BOG24) obviously had lower numbers of inhabitants (Appendix 1). These may have been at stages just after the colony foundation (cf. Sudd and Franks 1987). Data for other colonies show that as a colony grows in terms of the number of nests per colony, the number of colony members increases dramatically (Appendix 1), as suggested by Oster and Wilson (1978). In this subsequent stage, profits are mainly re-invested in workers and infrastructure such as the nest (Sudd and Franks 1987).

At some critical size, a colony begins to produce sexual offspring in order to realize its inclusive fitness. In our case even the 2-nest colony had already produced some males. But there was no relation between the colony size and number of males present. For example, in the 12-nest colony (BOG25), the number of males was relatively small as compared with BOG38 and BOG10 with fewer nests. Several factors may be responsible for this. Some males might have already left the nest when it was collected. Furthermore we do not know whether males are produced throughout the year or during restricted seasons.

The increase in queen number may increase the size of the colony, and finally the number of reproductives. Although in this study queen number positively affected the number of workers and immatures, the relationship between queen number and new queen (also male) number was not positive. This shows that other factors may have operated in determining the development of queens and males as reported for many other genera (for the Argentine ant, see Aron et al. 2001). In *M. arachnoides* maintaining a large worker force on one tree itself may be important under certain conditions (e.g., presence of competitors) at the cost of producing more reproductives. Furthermore we cannot know how many reproductives have been produced in a colony at the time of collection because dispersed individuals do not leave any indication of their previous presence in the colony unlike the case for social vespids where reproductive production can be measured rather precisely by observing pupal remnants.

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Appendix 1. Composition of life forms (stages) in colonies and nests.

	Nest	Nest & Leaf Measure	W	Q	WQ	M	Egg	Larva	WorkerP	MaleP	QueenP	Total
BOG24	Nest 1	N:5.0×7.5 cm L:7.7×24.5 cm	880	3	0	0	954	209	81	0	0	2127
BOG3	Nest 1	N:5.0×11.0 cm L:5.5×16.9 cm	549	1	2	38	257	390	7	4	0	1248
	Nest 2	N:7.0×12.0 cm L:10×17.0 cm	607	3	2	58	324	359	1	0	0	1354
	Subtotal		**1156**	**4**	**4**	**96**	**581**	**749**	**8**	**4**	**0**	**2602**
BOG18	Nest 1	N:14.5×16.0 cm L:22.0×28.0 cm	1780	22	38	69	1156	1039	1		0	4105
	Nest 2	N:10.0×14.5 cm L:26.0×27.5 cm	1413	13	14	86	929	657	39	5	0	3156
	Nest 3	N:NR L:NR	15	0	0	2	0	0	0	0	0	17
	Subtotal		**3208**	**35**	**52**	**157**	**2085**	**1696**	**40**	**5**	**0**	**7278**
BOG26	Nest 1	N:5.5×9.5 cm L:8.2×23.5 cm	415	7	0	6	820	214	91	1	0	1554
	Nest 2	N:4.5×8.8 cm L:6.0×17.0 cm	436	10	0	1	871	187	32	1	0	1538
	Nest 3	N:3.8×6.0 cm L:5.8×18 cm	278	1	0	3	104	43	1	0	0	430
	Subtotal		**1129**	**18**	**0**	**10**	**1795**	**444**	**124**	**2**	**0**	**3522**
BOG38	Nest 1	N:5.0×9.5 cm L:10.3×29.2 cm	335	2	3	36	75	61	17	12	0	541
	Nest 2	N:3.2×6.3 cm L:5.7×17.5 cm	62	1	0	6	85	105	9	2	0	270
	Nest 3	N:5.5×7.5 cm L:7.5×19.0 cm	212	1	0	20	147	274	44	6	0	704
	Subtotal		**609**	**4**	**3**	**62**	**307**	**440**	**70**	**20**	**0**	**1515**
BOG10	Nest 1	N:7.8×11.0 cm L:NR	417	2	3	64	719	295	69	1	0	1570
	Nest 2	N:6.0×9.0 cm L:NR	256	3	6	11	58	31	0	0	0	365
	Nest 3	N:6.0×12.0 cm L:3.5×16.0 cm	489	4	3	108	299	186	48	3	0	1140
	Nest 4	N:8.0×11.5 cm L:6.5×16.0 cm	956	7	11	139	661	312	14	0	0	2100
	Subtotal		**2118**	**16**	**23**	**322**	**1737**	**824**	**131**	**4**	**0**	**5175**
BOG25	Nest 1	N:5.5×14.0 cm L:7.5×36.5 cm	655	3	0	6	658	746	186	1	0	2255
	Nest 2	N:8.0×20.0 cm 6.0×16.5 cm L:9.0×48.0 cm	1380	7	0	12	1586	1260	339	3	0	4587
	Nest 3	N:6.0×26.0 cm L:9.5×34.5 cm	1259	6	1	7	1107	1100	363	3	0	3846
	Nest 4	N:6.5×20.0 cm L:9.5×31.cm N:5.0×12.5 cm L:7.0×18.0 cm	1437	9	0	6	1843	1545	321	7	0	5168
	Nest 5	N:6.5×16.0 cm L:9.5×44.0 cm	534	4	1	34	461	214	63	0	0	1311
	Nest 6	N:6.0×17.0 cm L:12.0×30.5 cm	714	2	0	1	610	503	157	0	0	1987

Appendix 1. Continued.

Nest	Nest & Leaf Measure	W	Q	WQ	M	Egg	Larva	WorkerP	MaleP	QueenP	Total
Nest 7	N:5.3×18.5 cm L:9.5×40.5 cm	617	4	0	0	632	224	120	2	0	1599
Nest 8	N:7.0×19.0 cm L:9.4×32.0 cm	1205	12	0	14	1658	1613	138	5	0	4645
Nest 9	N:5.5×14.5 cm L:8.5×27.0 cm	413	2	0	1	91	528	63	0	0	1098
Nest 10	N:6.5×12.5 cm L:7.8×20.5 cm	662	4	0	2	481	393	45	0	0	1587
Nest 11	N:6.0×16.0 cm L:9.3×36.0 cm	722	0	0	1	516	455	121	2	0	1817
Nest 12	N:7.0×19.0 cm L:9.8×28.5 cm	968	3	0	3	794	460	194	2	0	2424
Subtotal		**10566**	**56**	**2**	**87**	**10437**	**9041**	**2110**	**25**	**0**	**32324**

W=worker, Q=queen, WQ=winged queen, M=male, WorkerP=worker pupa, MaleP=male pupa, QueenP=queen pupa, NR=not recorded, N=nest, L=leaf.